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Responses of Strawberry Species and Cultivars to the Root-lesion and Northern Root-knot Nematodes

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Abstract. **The relative susceptibility of 44 genotypes of wild *Fragaria* L. and commercial cultivars of strawberry *Fragaria ×ananassa* Duch. to *Meloidogyne hapla* Chitwood and *Pratylenchus penetrans* (Cobb) Filipjev & Shuurmans Stekhoven was evaluated in the greenhouse. Eleven genotypes were highly resistant to populations of *M. hapla* from Washington State and Oregon, with Rf values (initial nematode density/final population density) less than 0.5. However, root growth of most genotypes, including resistant genotypes, was reduced by *M. hapla.* Thirteen genotypes were ranked more resistant to *P. penetrans* than *F. ×ananassa* 'Totem', a susceptible cultivar. Root growth of most genotypes was not affected by *P. penetrans* under these experimental conditions. We conclude that commercial cultivars and wild *Fragaria* genotypes can provide a readily exploitable source of resistance to *M. hapla.* Conversely, sources of resistance to *P. penetrans* were uncommon in the germplasm evaluated. The *F. ×ananassa* cultivars, which already have commercially important characteristics, appear to be a better source of resistance for both nematode species than the wild, unimproved germplasm.**

Plant-parasitic nematodes can affect the growth and development of strawberry resulting in economic loss. Genera of phytonematodes modify root growth and function (*Meloidogyne, Xiphinena,* and *Longidorus*), induce root necrosis (*Pratylenchus*), deform and stunt leaves and shoots (*Aphelenchoides*), vector NEPO viruses (*Xiphimena,* and *Longidorus*), and interact with soilborne fungal and bacterial pathogens (*Pratylenchus* and *Meloidogyne*) (Brown et al, 1993; Esnard and Zuckerman, 1998). Currently, phytonematodes are controlled by preplant fumigation and/or post-plant applications of nonfumigant nematicides. However, these management options may not be available in the future. Methyl bromide, the most effective fumigant, is being phased out of use because of regulations that document its role in depletion of the ozone layer (Clean Air Act, 1990). Methyl bromide will be available in limited quantities after 2005 only for approved critical uses that do not have technically or economically feasible alternatives. Registration and use of many nematicides in minor crops also may be limited because of provisions in the Food Quality Protection Act (1996). The introduction of strawberry cultivars that are tolerant and/or resistant to phytonematodes should decrease the reliance on nematicides to maintain the productivity of plants in nematode-infested soils.

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Meloidogyne hapla Chitwood (northern root-knot nematode) and *Pratylenchus penetrans* (Cobb) Filipjev & Shuurmans Stekhoven (root-lesion nematode) are important pests in strawberry production worldwide (Brown et al. 1993; Esnard and Zuckerman, 1998). *Meloidogyne hapla* second-stage juveniles penetrate the tips of young roots where they cause small galls and the proliferation of adventitious rootlets (Edwards et al., 1985). The physiology and water relations of infected plants are disrupted and may result in severe stunting in sandy soils. *Pratylenchus penetrans* is an endoparasite that migrates through and feeds in the root cortex (Townshend, 1963a). These activities kill the surrounding root tissues, which become visible as discrete necrotic lesions. When high *P. penetrans* population densities are present, the lesions may coalesce and girdle the roots. The above ground symptoms of infected strawberry plants are similar for both nematode species; stunting, reduced runner production, depressed yields, and shortened life of the planting. In addition to the direct damage *P. penetrans* and *M. hapla* cause, both species have been implicated in disease complexes affecting strawberry (Abu-Gharbieh et al, 1962; Kurppa and Vrain, 1989; Martin, 1988; Szczygiel and Profic-Alwasiak, 1989).

Plant resistance is the ability of a plant to suppress nematode development and reproduction (Roberts, 2002). Plant tolerance is the ability of a plant to withstand nematode infection without the loss of plant growth or productivity (Roberts, 2002). Host plant resistance and/or tolerance have been proven a cost-effective strategy for managing plant-parasitic nematode that affect agronomic and horticultural crops (Young, 1998). This approach has potential for management of nematode damage in strawberry. Orchard and Andrichem (1961) observed differential root galling and egg mass production in eleven *Fragaria* species and subspecies that were planted in soil infested with *M. hapla.* Similarly, Dickstein and Krusberg (1978) reported that 33 strawberry cultivars differed considerably in their galling response to *M. hapla.* Based on the fresh biomass of 46 strawberry cultivars in several greenhouse studies, 'Earliglow' (Edwards, et al. 1985) and 'Glima' and 'Senga Sengana' (Szczygiel, 1981a) were tolerant or highly resistant to *M. hapla.* Szczygiel (1981b) also found 'Senga Sengana' to be the most resistant and tolerant to *P. penetrans* among 28 cultivars evaluated. Potter and Dale (1994; Dale and Potter, 1998) reported resistance and tolerance to *P. penetrans* among *Fragaria chiloensis* (L.) Duch. and *F. virginiana* Duch. genotypes and *F. ×ananassa* cultivars. Based on their work with a limited number of genotypes, they concluded that resistance to *P. penetrans* can be increased in cultivated strawberries by introducing wild germplasm and that further screening of *Fragaria* germplasm is warranted. Moreover, research data cited above suggests that screening for resistance to *M. hapla* should be profitable.

Hancock et al. (2001a, 2002) have identified a supercore group of native *F. virginiana* and *F. chiloensis* clones that represent the broad distribution of the octoploid species in North and South America. Further, they have focused various *Fragaria* germplasm evaluation projects on this supercore (Hancock et al. 2001b).

The objective of this study was to evaluate an elite group of strawberry accessions for resistance and tolerance to *M. hapla* and *P. penetrans.* Accessions were primarily from the supercore (Hancock et al, 2001a) of subspecies of *F. chiloensis* (L.) Miller and *F. virginiana* Miller along with *F. ×ananassa* cultivars that are important in production areas of North America

Materials and Methods

Native octoploid strawberries were propagated vegetatively at the USDA–ARS Horticultural Crops Research Laboratory, Corvallis, Ore. Plants not available at the HCRL were obtained from the USDA–ARS National Clonal Germplasm Repository in Corvallis and Jim Hancock at Michigan State University, East Lansing. Several cultivars were obtained as bare root plants from commercial nurseries. Plants of each genotype were kept in a greenhouse under long day conditions (16-h photoperiod) with 24 °C day and 18 °C night temperatures. In March through April, runners were pegged into four inch pots containing about 800 g of steam pasteurized sandy soil (1:2 by volume, washed sand and Willamette loam). Once established, the rooted daughter plants were cut from the mother plant and grown in the greenhouse.

Genotypes varied in initiation of runners and development of daughter plants, with some genotypes requiring an additional month to reach the size desired for the experiment.

Because of differential development of plants and the space constraints in extracting nematodes from soil and root tissue, genotypes were divided into three groups based on plant development to obtain plants of similar size for each run. Those genotypes that produced runners and rooted the quickest were screened in the first run, while the slower growing genotypes were included in the third run.

The population of *P. penetrans* used in the study was collected in a peppermint (*Mentha piperita* L. 'Todd') field in Harrisburg, Ore. Nematodes were extracted from peppermint roots and used to infest pasteurized loam: sand containing 'Totem' strawberry plants in greenhouse pot cultures (Forge et al. 2000). After nine months, nematodes were collected from the strawberry roots and used to infect new nematode-free peppermint plants, which served as stock culture for all experiments. Populations of *M. hapla* (Mh) were collected from vineyards in Dundee, Ore. (MhO), and Benton City, Wash. (MhW). A tomato (*Lycoperisicon esculentum* Mill. 'Early Girl'), was planted in the vineyard soil mixed with loam:sand. After 6 months, egg masses were collected from tomato roots and used to infect 'Totem' strawberry greenhouse cultures. Specimens of female and second-stage juvenile (J2) nematodes were collected from the strawberry roots and examined to verify that the population was solely *M. hapla.* Stock cultures of *M. hapla* on tomato were started with egg masses collected from strawberry roots.

Nematodes used to infect the *Fragaria* genotypes were extracted from the roots of stock cultures immediately before they were needed. Peppermint roots were washed free of soil and placed under intermittent mist to extract *P. penetrans* (Ayoub, 1981). Nematodes were collected daily and stored in water two days or less at 4 °C before infesting soil. Eggs of *M. hapla* were extracted from roots of tomato cultures using a NaOCl method (Hussey and Barker, 1973). The density of nematodes or eggs in the suspensions used to infest the soil was adjusted to 75/mL for *P. penetrans* and 200 eggs/mL for *M. hapla*. Four holes (1 cm diameter × 5 cm) were made around the crown of each plant, 5 mL of the nematode suspension was pipetted into each hole, and the holes were filled with soil mix. Infestation densities were 1500 *P. penetrans* per pot (2/g soil) or 4000 *M. hapla* eggs per pot (5/g soil).

Twenty-four plants of each genotype were selected for uniformity and three plants of similar size were selected for each replication. Two plants were infested with either *P. penetrans* or *M. hapla*, while the third plant in the replication was a noninfested control. Experimental design was randomized block with eight replications. Plants infested with *M. hapla*, *P. penetrans* and noninfested controls were blocked in each replication and separated with fiberglass barriers to prevent cross-contamination. The experiment was conducted in a greenhouse with supplementary light (16-h photoperiod) and temperature maintained between 18 to 26 °C. Plants were fertilized with 15–5–15 Cal-Mag (Scott Co., Maryville, Ohio) biweekly. The three groups or runs of genotypes were infested with nematodes at 2-week intervals; on 22 June, 6 July, and 20 July 2000. Because the mist-chamber malfunctioned in the first run and *P. penetrans* extracted from the roots were lost, these genotypes were evaluated again in 2001. Plants were infested on 26 July 2001 for run 4. Plants were not available for RH 30, NC 95-19-1, CFRA 440, and CFRA 368 genotypes, so they were not evaluated for response to *P. penetrans*. Those genotypes that showed resistance to MhO in 2000, were evaluated with the MhW population in July 2001. 'Totem' was selected as the standard in each run because it has been shown to be good host for *M. hapla* (Pinkerton, unpublished data) and *P. penetrans* (Forge et al., 2000) and it accounts for 90% of strawberry production in the Pacific Northwest. At least two other genotypes were repeated in two more runs. 'Early Girl' tomatoes served as a control for viability of *M. hapla* inoculum in each run.

Twelve weeks after infestation of the soil, plants were cut off at the soil line, the shoots were oven-dried at 50 °C, and the tissue weighed. At this time, the root system was shaken carefully and brushed to remove soil. A 100-g soil sample from each pot was processed by the Baermann funnel method (Townshend, 1963b) to extract the vermiform stages of both nematode species. Initially the roots were washed free of soil by submerging them in water and then carefully washing them in a gentle stream of water. Root systems of plants infected with *P. penetrans* were placed under intermittent mist for 7 d to extract the nematodes. Roots infected with *M. hapla* were inspected under a dissecting microscope for the presence of galls. A gall rating was assigned to each root system; 0 = no galls, 1 = 1 to 2 galls, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 = >100 galls (Taylor and Sasser, 1978). Each root system was then cut into 2 to 4 cm pieces and eggs were extracted in NaOCl as described by Hussey and Barker (1973). Nematode eggs collected in a 28-μ sieve were rinsed into a beaker from which a 1-mL sample was drawn to count the eggs. After extracting the nematodes or eggs, roots were oven-dried at 50 °C and the tissue weighed.

Plant resistance was expressed the reproductive factor (Rf = final population density [eggs and/or vermiform stages]/initial nematode population density). To standardize the data between the runs, data also were expressed as the relationship of the Rf value of each nematode species on each genotype to its Rf value on 'Totem' in each replication (genotype Rf/Totem Rf). The mean gall rating for *M. hapla* and the number of *P. penetrans*/g root also were calculated. *Pratylenchus penetrans*/g root was transformed, $\log_{10}(x + 1)$, before statistical analysis. Plant tolerance was expressed as the ratio of plant dry weights between paired infected and noninfected plants in each replication (infected weight/noninfected weight). Tolerance ratio values were calculated for root and total plant dry weights. Model variance components were estimated using ANOVA procedures and means separated by Fisher's protected LSD (Statgraphics, version 3, Manugistics Inc., Rockville, Md., 1997).

Results

Meloidogyne hapla trials. Gall rating, Rf × 'Totem', and root and shoot tolerance ratio values were not different ($P \leq 0.05$) between the MhO and MhW populations. Therefore, data were combined for analysis of variance.

Fragaria subspecies segregated to three groups by root galling (Table 1); *F. virginiana subsp. virginiana* (south) and *F. ×ananassa* had the lowest gall ratings ($P \leq 0.001$), *F. virginiana* subsp. *virginiana* (north), *F. chiloensis* subsp. *chiloensis,* and *F. virginiana* subsp. *glauca* had intermediate ratings, and *F. chiloensis* subsp. *pacifica*, *F. virginiana* subsp. *platypetala*, and *F. chiloensis* f. *patagonica* subsp. *chiloensis* had the most galling. Gall rating values were similar between runs for genotypes tested in multiple runs. For example, gall rating values for 'Totem' ranged between 4.25 and 5.0. Fifteen genotypes infected with MhO had gall ratings <1.0 and of those genotypes retested with MhW, only NC 96-48-1, JP 95-1-1, and 'Jewel' had gall ratings >1.0.

Nematode reproduction on *Fragaria* genera corresponded to gall ratings (Table 1). The Rf values of genera segregated to three groups in which *F. virginiana* subsp. *glauca* and *F. virginiana* subsp. *virginiana* (south) had the lowest values and *F. virginiana* subsp. *virginiana* (north) and *F. chiloensis* subsp. *pacifica* had the greatest Rf values. 'Totem' was among the most susceptible genotypes with mean Rf values greater ($P \leq 0.01$) for MhW (52.9) than for MhO (15.1). However, reproduction was not different between *M. hapla* populations for most genotypes. Of the 14 genotypes that had mean Rf values ≤1.0 with MhO, 3 had Rf values >3 when retested with MhW and of these only JP 95-1-1 had a significantly greater ($P \leq 0.01$) Rf value (12.6) with MhW. After standardizing Rf values of genotypes relative to 'Totem', genotypes with Rf values <1.0 also were the most resistant compared to 'Totem' with Rf × T values <0.1. Mean Rf values for 'Early girl' tomato ranged from 76 to 233 among runs.

Root biomass of 20 genotypes was reduced significantly ($P < 0.05$) in plants infected with *M. hapla* compared to noninfected control plants (Table 1); the mean reduction of all genotypes was 69% (tolerance ratio = 0.69). Root growth of 'Totem' was reduced 10 to 33% in the four runs, while root mass was reduced >25% in 24 genotypes. However, the reduction in root mass was not correlated ($P \leq 0.05$) with gall rating, Rf value, or eggs/g root (data not presented). Total plant weights of 15 genotypes was reduced ($P \leq 0.05$) for plants infected with *M. hapla* compared with noninfected plants (Table 1).

Pratylenchus penetrans trials. The Rf values ranged from 0.06 to 1.32 (Table 2). 'Totem' had an intermediate Rf value (0.33) among the genotypes with only 13 genotypes having the Rf × 'Totem' values <1.0. The Rf values of genotypes tested in more than one run did not differ ($P = 0.093$). Nematodes per gram root ranged from 18 to 1400, with 'Totem' intermediate (95.4). Among the eight taxon groupings, reproduction of *P. penetrans* was the greatest

($P \leq 0.001$) on *F. chiloensis* subsp. *pacifica* and *F. virginiana* subsp. *platypetala* and the lower for all other *Fragaria* taxa (Table 2). *Fragaria chiloensis* subsp. *pacifica* and *F. virginiana* subsp. *platypetala* genotypes had the greatest nematodes/g root ($P \leq 0.001$), *Fragaria chiloensis* f. *patagonica* subsp. *chiloensis* genotypes were intermediate, and the other genera had the fewest nematodes in the roots.

Table 1. Taxa and genotype means for gall rating, reproductive factor (Rf)[z], reproductive factor of genotypes compared to 'Totem', and tolerance ratio values of root and whole plant biomass of strawberry genotypes infected with *Meloidogyne hapla* grown in greenhouse pots for 12 weeks.

Species	Taxon	No. of genotypes	Rf	Rf × Totem[y]	Gall rating[x]		
Fragaria chiloensis subsp. *pacifica*	FCP	7	14.26 d[w]	1.16 d	3.7 de		
F. chiloensis subsp. *f. chiloensis*	FCC	4	4.16 abc	0.31 ab	3.4 cd		
F. chiloensis f. patagonica subsp. *chiloensis*	FCPC	4	8.33 bc	0.66 ab	4.1 e		
F. virginiana subsp. *glacua*	FVG	2	0.90 a	0.13 a	2.4 cd		
F. virginiana subsp. *platypetala*	FVP	4	8.82 bc	0.76 abc	4.0 e		
F. virginiana subsp. *virginiana* (North)	FVVN	6	11.72 d	1.03 ab	3.3 cd		
F. virginiana subsp. *virginiana* (South)	FVVS	6	1.92 ab	0.08 a	0.8 a		
F. ×ananassa	FA	11	3.64 ab	0.20 ab	1.3 b		
Significance (*P*)			0.001	0.001	0.001		
Genotype[v]	Taxon	PI NO[v]	Rf	Rf × Totem	Gall rating	Root tolerance[u]	Total plant tolerance[u]
Camarosa	FA		0.01 a	0.00 a	0.0 a	0.55	1.04
NC95-21-1	FVVS	612569	0.01 a	0.00 a	0.0 a	0.79	0.83
NC 96-35-2	FVVS	612323	0.02 a	0.00 a	0.0 a	0.85	1.02
Chandler	FA		0.04 a	0.00 a	0.0 a	0.90	0.82
NC 96-5-3	FVVS	612325	0.05 a	0.01 a	0.0 a	0.98	1.19
LH 50-4	FVG	612495	0.07 a	0.01 a	0.1 a	0.91	0.84
Allstar	FA	551406	0.08 a	0.01 a	0.1 a	0.94	0.92
Firecracker	FA	617006	0.09 aa	0.01 a	0.1 a	0.79*	0.83
Fred 9	FVVN	612493	0.14 a	0.01 a	0.0 a	0.70*	0.7
NC 95-19-1	FVVS	312486	0.15 ab	0.02 abc	0.1 a	0.83	0.95
Diamante	FA		0.32 ab	0.05 abc	1.5 bc	0.82	0.86
CFRA 24	FCC	236579	0.83 ab	0.13 abdc	0.7 ab	0.62*	0.96
Redcrest	FA	551859	0.98 abc	0.04 abc	0.4 a	0.88	0.92
MS 30-21	FVVN		1.00 abcd	0.06 abdc	2.1 cde	0.68	0.86
CFRA 372	FCC	551736	1.18 abcd	0.07 abdc	3.8 ghi	0.66	0.90
Puget Reliance	FA		1.27 abcd	0.14 abdc	1.4 bc	0.71*	0.55
Honeoye	FA	551588	1.56 abcd	0.06 abc	0.0 a	0.86	0.87
CFRA 338	FVG	551745	1.73 abcd	0.24 abcdef	4.6 ijk	0.79	0.95
CFRA 1088	FCPC	612316	1.98 abcd	0.21 abcdef	4.3 hijk	0.41*	0.73*
CFRA 42	FCP	551453	2.26 abcd	0.34 abcdefg	2.0 cd	0.33*	0.58*
CFRA 368	FCP	551735	2.28 abcd	0.18 abcdef	3.5 fgh	0.49*	0.63*
MS 9-7	FVVN		2.31 abcd	0.14 abcde	3.0 efg	0.91	0.71*
CFRA 1092	FCPC	612317	2.75 abcd	0.27 abcdef	3.9 ghij	0.55*	0.94
ORUS 1484-1	FCC	616767	2.75 abcde	0.32 abcdefg	4.4 hijk	0.92	1.30*
CFRA 101	FVP	551518	3.26 abcde	0.74 fghi	4.3 hijk	0.56*	0.62*
Jewel	FA		3.35 abcde	0.26 abcdef	1.6 c	0.68*	0.84*
NC 96-48-1	FVVS	612324	4.75 abcde	0.31 abcdef	2.2 cde	0.64*	0.79
JP 95-1-1	FVVS	612570	6.53 abcdef	0.16 abcde	2.7 def	0.59*	0.80*
Scotts Creek	FCPC	612490	6.56 abcdef	0.23 abcdef	2.6 def	0.64	0.77*
ORUS 1414-1	FA		7.69 bcdefg	0.58 cdefg	4.6 ijk	0.67	0.87
CFRA 110	FVP	551527	8.31 cdefg	0.16 abcde	3.9 ghij	0.48*	0.60*
CFRA 440	FVP	551794	8.52 cdefg	0.83 fghij	3.5 fgh	0.47*	0.54*
CFRA 1100	FCPC	602548	9.17 defg	0.97 ghij	4.9 jk	0.75	1.14
Eagle 14	FVVN	612492	11.10 efgh	0.55 bcdefg	4.9 jk	0.68*	0.87
HM1	FCPC	612489	11.46 efgh	1.49 j	4.0 hijk	0.80	0.88
CFRA 688	FCPC	612487	12.80 fgh	0.69 defghi	4.3 hijk	0.50*	0.71
CFRA 796	FCPC	552091	13.60 fgh	0.73 efghi	4.9 jk	0.54*	0.82
NAH 5-1	FCC		13.66 fgh	0.72 efghi	4.9 jk	0.79	0.88
CFRA 58	FVP	551471	15.19 gh	1.29 hij	4.4 hijk	0.54	0.77
CFRA 34	FCP	551445	18.62 hi	1.33 ij	4.4 hijk	0.50	1.01
RH 23	FVVN	612498	24.27 ij	2.56 k	4.9 jk	0.81	0.83*
Totem	FA	551501	24.66 ij	1.00 ghij	4.7 jk	0.95*	0.85*
RH 30	FVVN	612499	31.50 jk	2.84 k	5.0 k	0.54*	0.69
CFRA 1267	FCP	612488	33.88 k	2.80 k	5.0 k	0.57*	0.93
Significance (*P*)							
Genotype			0.001	0.001	0.001		
Run[t]			0.650	0.059	0.003	0.085	0.20

[z]Rf = final population density/initial nematode population density.
[y]Rf × Totem values are means of the Rf on plants of a genotype/Rf of 'Totem' in each replication.
[x]Gall rating 0 = no galls, 1 = 1 to 2 galls, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 = >100 galls
[w]Values within a column followed by the same letter are not different according to Fisher's protected LSD ($P \leq 0.05$).
[v]Sources of plant material; Plants with a PI (plant introduction) number are currently in the repository system, ORUS = selection from USDA–ARS (Corvallis, Ore.) program; MS = accession from University of Minnesota. NAH 5-1 was collected in the same community in Ecuador as NAH 3(PI 612318) and may be the same clone (Finn et al., 1998).
[u]Tolerance ratio value for a genotype is the mean of dry weights of tissues of infected plants/dry weights of tissues of noninfected plants in each replication. Asterisks indicate that dry weights of infected tissues differed ($P \leq 0.05$) from tissues of noninfected plants.
[t]Analysis of runs is only for the genotypes that were included in more than one run ($P \leq 0.05$).

Pratylenchus penetrans had less affect on root growth than did *M. hapla* (Table 2). Mean tolerance ratio value was 0.95 among all genotypes. Root growth was reduced by *P. penetrans* in four and increase in three genotypes ($P \leq 0.05$), while root biomass of other genotypes was not affected significantly by *P. penetrans*. *Pratylenchus penetrans* had little effect on total plant biomass with mean tolerance ratio value of 1.02 among genotypes.

Discussion

Dickstein and Krusberg (1978), Edwards et al. (1985) and Szczygiel (1981a) reported that *M. hapla* galled roots and/or reproduced

Table 2. Taxa and genotype means for reproductive factor (Rf)[z], reproductive factor of genotypes compared to 'Totem', nematodes per gram root, and tolerance ratio values of root and total plant biomass of strawberry genotypes infected with *Pratylenchus penetrans* and noninfected control plants grown in greenhouse pots for 12 weeks.

Species	Taxon	No. of genotypes	Rf	Rf × Totem[y]	Nematodes/ g root[x]
Fragaria chiloensis subsp. *pacifica*	FCP	6	0.76 b[w]	2.71 b	582 e
F. chiloensis subsp. *f. chiloensis*	FCC	4	0.19 a	0.86 a	83 ab
F. chiloensis f. patagonica subsp. *chiloensis*	FCPC	4	0.32 a	1.41 a	268 cd
F. virginiana subsp. *glacua*	FVG	2	0.26 a	1.35 a	76 a
F. virginiana subsp. *platypetala*	FVP	3	0.59 b	2.86 b	348 de
F. virginiana subsp. *virginiana (North)*	FVVN	5	0.26 a	1.52 a	97 ab
F. virginiana subsp. *virginiana (South)*	FVVS	5	0.30 a	1.25 a	146 bc
F. ×ananassa	FA	11	0.30 a	1.01 a	89 ab
Significance (*P*)			0.001	0.001	0.001

Genotype[v]	Taxon	PI NO[v]	Rf	Rf × Totem	Nematodes/ g root	Root tolerance[u]	Total plant tolerance[u]
CFRA 372	FCC	551736	0.06 a	0.48 a	30.1 abc	0.88	0.95
Firecracker	FA	617006	0.07 a	0.54 a	19.2 ab	0.91	0.69
CFRA 1092	FCPC	612317	0.08 a	0.48 a	35.7 abcde	1.02	1.13*
Eagle 14	FVVN	612492	0.08 a	0.45 a	17.8 a	1.05	1.04
NAH 5-1	FCC		0.09 a	0.74 abc	30.2 abc	0.98	0.87
Diamante	FA		0.09 a	0.43 a	18.4 ab	1.19*	1.28
ORUS 1414-1	FA		0.10 ab	1.04 abcd	35.1 abcd	0.99	1.04
JP 95-1-1	FVVS	612570	0.13 abc	1.30 abcde	104.2 defghi	0.77	0.94
Scotts Creek	FCP	612490	0.15 abc	2.00 abcdefgh	34.3 abcd	0.97	0.97
Allstar	FA	551406	0.17 abcd	0.86 abcd	32.6 abcd	1.03	0.96
Chandler	FA		0.18 abcd	0.60 ab	30.3 abc	1.12	0.93
ORUS 1484	FCC	616767	0.19 abcde	0.82 abc	97.2 defghi	0.95	1.24*
NC 96-5-3	FVVS	612325	0.19 abcde	0.61 abc	80.0 cdefhgi	0.87	1.00
MS 30-21	FVVN		0.20 abcde	1.78 abcdefg	54.5 cdef	1.08*	1.05
NC95-21-1	FVVS	612569	0.21 abcdef	1.43 abcde	72.6 cdefg	1.08	1.20*
MS 9-7	FVVN		0.22 abcdef	1.31 abcde	44.8 bcdef	1.01	1.11
CFRA 338	FVG	551745	0.23 abcdef	1.08 abcd	76.9 cdefg	1.08	1.28
NC 96-35-2	FVVS	612323	0.23 abcdef	0.95 abcd	60.7 cdefg	1.09	1.39*
Jewel	FA		0.28 abcdefg	0.71 abc	74.8 cdefg	0.81	0.98
LH 50-4	FVG	612495	0.30 abcdefg	1.62 abcdef	75.5 cdefg	1.17	1.32*
CFRA 796	FCPC	552091	0.31 abcdefg	2.46 bcdefgh	186.2 ghijk	1.02	1.10
Fred 9	FVVN	612493	0.32 abcdefg	2.26 bcdefgh	145.0 fghij	0.79	0.97
CFRA 1100	FCPC	602548	0.32 abcdefg	0.99 abcd	100.1 defghi	1.05	1.38*
Totem	FA	551501	0.33 abcdefg	1.00 abcd	95.4 cdefhgi	1.05	0.99
Honeoye	FA	551588	0.35 abcdefg	1.17 abcd	62.6 cdefg	1.09	1.04
CFRA 110	FVP	551527	0.36 abcdefgh	3.79 h	129.7 fghij	0.93	0.91
CFRA 24	FCC	236579	0.41 bcdefgh	1.38 abcde	173.7 ghijk	1.00	1.04
Camarosa	FA		0.46 bcdefghi	1.46 abcde	129.4 fghij	1.17*	1.30*
RH 23	FVVN	612498	0.49 cdefghi	1.81 abcdefg	221.1 ghijk	1.15	1.04
Redcrest	FA	551859	0.51 defghi	1.23 abcde	183.9 ghijk	0.97	1.00
CFRA 42	FCP	551453	0.54 efghi	1.29 abcde	501.4 klmn	0.64*	0.82
CFRA 688	FCP	612487	0.56 fghi	3.75 h	298.5 ijklm	0.60*	0.77
CFRA 1088	FCPC	612316	0.57 ghi	1.72 abcdef	750.4 mn	1.09	0.82
CFRA 101	FVP	551518	0.69 hij	3.15 fgh	259.3 hijkl	0.61	0.87
CFRA 58	FVP	551471	0.70 hijk	1.65 abcdef	656.2 lmn	0.79	0.87
Puget Reliance	FA		0.76 ijk	2.04 abcdefgh	295.8 ijkl	0.76	0.89
NC 96-48-1	FVVS	612324	0.76 ijk	1.98 abcdefgh	413.8 jklm	0.77	0.90
HM1	FCP	612489	0.95 jk	2.82 defg	470.6 klmn	0.97	1.14
CFRA 34	FCP	551445	1.02 kl	2.74 defg	783.5 mn	0.57*	0.89
CFRA 1267	FCP	612488	1.32 l	3.66 gh	1404.1 n	0.83*	0.91
Significance (*P*)							
Genotype			0.001	0.001	0.001		
Run[t]			0.093	0.673	0.001	0.001	0.001

[z]Rf = final population density/initial nematode population density.
[y]Rf × 'Totem' values are means of the Rf on plants of a genotype/Rf of 'Totem' in each replication.
[x]Mean nematode densities per gram dry weight root was detransformed from log 10 (x + 1) for statistical analysis.
[w]Values within a column followed by the same letter are not different according to Fisher's protected LSD ($P \leq 0.05$).
[v]Sources of plant material; Plants with a PI (plant introduction) number are currently in the repository system, ORUS = selection from USDA–ARS (Corvallis, Ore.) program; MS = accession from University of Minnesota. NAH 5-1 was collected in the same community in Ecuador as NAH 3(PI 612318) and may be the same clone (Finn et al., 1998).
[u]Tolerance ratio value for a genotype is the mean of dry weights of tissues of infected plants per dry weights of tissues of noninfected plants in each replication. Asterisks indicate that dry weights of infected tissues differed ($P \leq 0.05$) from tissues of noninfected plants.
[t]Analysis of runs is only for the genotypes that were included in more than one run ($P \leq 0.05$).

well on most strawberry cultivars tested, with several cultivars showing similar responses in different studies. Edwards et al. (1985) reported that 4 of 11 and Szczygiel (1981a) reported 2 of 25 *F.* ×*ananassa* cultivars evaluated were resistant to *M. hapla.* We observed a high degree of resistance to *M. hapla* among a diverse collection of *Fragaria* genotypes, with Rf values <0.5 for 11 of the 44 genotypes tested. Of the *F.* ×*ananassa* cultivars evaluated in our study, 'Camarosa', 'Chandler', Allstar', Firecracker', and 'Dimante' were highly resistant to *M. hapla.* Orchard and Andrichem (1961) observed differential galling of roots among 11 *Fragaria* species and subspecies. They noted resistance in one genotype of *F. virginiana* subsp. *platypetala*. However, we observed no resistance in the four genotypes of *F. virginiana* subsp. *platypetala* or six genotypes of *F. chiloensis* f. *patagonica* subsp. *chiloensis*. Genotypes of the other taxa varied from resistant to highly susceptible. We expect that the variability in nematode resistance within a *Fragaria* taxon would increase in proportion to the number of populations of that taxon evaluated. Although plant genotypes may respond differentially to different populations of a species of plant-parasitic nematode (DeWaele and Elsen, 2002; Roberts, 2002), in the current research all but three *Fragaria* genotypes had similar levels of resistance to an Oregon and a Washington population of *M. hapla.* Our data suggest resistance to *M. hapla* in *F.* ×*ananassa* cultivars should be easily exploited by strawberry breeders.

Tolerance is more difficult to demonstrate than resistance. It is especially difficult in greenhouse pot experiments in which plant roots are confined in a small volume of soil, soil is infested with high densities of nematodes, and in which water and nutrients are not limiting. Most genotypes were intolerant to *M. hapla* and plants grown in infested soil had less root mass than those in noninfested soil. This reduction in root growth was observed even with genotypes that had few galls or did not support population increase of *M. hapla*. Second-stage juveniles (J2) that penetrated the roots may have adversely affected root growth, but were not able to establish feeding sites and develop further. The high infestation density, 5 eggs/g soil, may have exacerbated the damage to roots, even in resistant genotypes. For example, *M arenaria* (Neal) Chitwood J2 penetrated resistant grape roots and caused hypersensitive reaction observed as necrosis of the root-tip (Anwar and McKenry, 2000). We observed that *M. hapla* affected the growth of roots more than total plant growth, i.e., among 44 genotypes the mean tolerance ratio value of total plant weight was 0.84. In contrast, Edwards at al. (1985) reported that *M. hapla* reduced root and total plant biomass of 11 *F.* ×*ananassa* cultivars to a similar degree.

Screening for host resistance and tolerance to migratory endoparasitic nematodes can be difficult compared to sedentary endoparasitic nematodes (DeWaele and Elsen, 2002; Peng and Moens, 2003). In our research, resistance of strawberry genotypes to *P. penetrans* was less common than resistance to *M. hapla.* The Rf values for *P. penetrans* ranged from 0.06 to 1.32, with the susceptible cultivar 'Totem' near the middle of the range at 0.33. These Rf values were lower than reported by other researchers. Potter and Dale (1994) evaluated the susceptibility of 20 genotypes of *F. virginiana* and 13 genotypes of *F. chiloensis* 16 and 20 weeks after infestation, respectively. There was a high degree of variability between populations of each species, with estimated Rf values ranging from 0.2 to 3.7. 'Midway' which was a good host in a previous study (Szczygiel, 1981b) did not support *P. penetrans* reproduction as well in their study with an estimated Rf value <0.39. Infestation density, plant size at infection, experimental conditions and duration, nematode sampling and extraction methods, and variability of nematode inocula may explain the differences in the estimated Rf values observed between experiments (DeWaele ad Elsen, 2002). For example, the duration of our experiments was 2 to 6 weeks shorter and nematode extraction period was 7 d shorter than those in the Potter and Dale study (1994). As with other studies (Potter and Dale, 1994), we observed great variability and few significant differences in resistance of *Fragaria* genotypes to *P. penetrans.* By comparing each genotype to the susceptible 'Totem' in each replication, some of the variability in our study was removed. There were only two genotypes in common between previous and current research, but these data were consistent with our data. *Pratylenchus penetrans* reproduced well on 'HM1' in our research and that of Potter and Dale (1994), while 'Chandler' was a poor host in both studies (Dale and Potter, 1998). A susceptible cultivar, 'Honeoye', used by LaMondia (1999, 2002) in several studies had a similar degree of resistance to 'Totem' in our study. Our data support the conclusions of Potter and Dale (1994) that there is a good level of resistance to *P. penetrans* available in *F.* ×*ananassa* cultivars without resorting to wild genotypes. They also reported that certain genotypes from the University of California breeding program had resistance to *P. penetrans* (Dale and Potter, 1998). This was supported by the good degree of resistance that we observed with 'Diamante' and 'Chandler'. Our data should serve to rank cultivars, and wild genotypes, as candidates in breeding for resistance to *P. penetrans.*

The Rf values of genotypes were correlated ($R^2 = 0.67$, $P \leq 0.01$) with *P. penetrans* per gram root tissue, which ranged from 18 to 1404 g/root. This range is similar to those observed on *Fragaria* genotypes and cultivars by other researchers (Goheen and Bailey, 1955; Kimpinski, 1985; LaMondia, 2002; Potter and Dale, 1994; Szczygiel, 1981b). Jaffee (1980) reported a negative correlation between root biomass at the time of infestation and the number of *P. penetrans* per gram root tissue. Genotypes of noninfected plants that produced the smallest root mass (<70% mean mass of all genotype) had among the highest number of nematodes per gram root in infected plants in our study, i.e., CFRA 24, CFRA 42, CFRA 58, CFRA 101, CFRA 1088, CFRA 1267, HM1, and RH 23. Therefore, the rooting habit and structure of a genotype should be considered when interpreting the level of resistance based on nematodes in the root tissue.

Szczygiel (1981b) reported a reduction in total plant biomass of plants infected with *P. penetrans* compared to noninfected plants for most of the 28 strawberry cultivars evaluated. In contrast, *P. penetrans* significantly reduced root biomass of only four genotypes and did not reduce significantly whole plant biomass of any genotype in our research. Several factors may account for apparent high degree of tolerance observed in our study. Older, large strawberry plants propagated from runners, as were the plants used in our research, may be more tolerant than young plants (Szczygiel, 1986). Tolerance may be associated with the plant growth conditions that vary with season and environmental conditions. Szczygiel (1983) reported that tolerance of 'Senga Sengana' strawberry to *P. penetrans* was 160 nematodes/g soil in the spring and 35/g in the summer and autumn-winter. Goheen and Smith (1956) reported that growth differences between infected and control plants decreased as plants became pot bound, as was the case with vigorous genotypes in our study. Because of low infection density of *P. penetrans* in the roots of most genotypes, plants may have compensated partially for nematode parasitism. Screening strawberry genotypes for tolerance to nematodes under field conditions or in microplot experiments over several years (Dale and Potter, 1998; LaMondia, 1999) would be a more robust evaluation than greenhouse pot experiments (DeWaele and Elsen, 2002).

Most plant resistance has been developed to sedentary endoparasitic nematodes that have co-evolved a highly specialized relationship with the host (Roberts, 2002). Root-knot nematodes induce changes in the plant at the cellular level that result in the formation of a specialized feeding site, the giant cell. Resistance mechanisms that disrupt this process may rely on a single or few genes. Conversely, the development of plant resistance to less-specialized parasites, such as *Pratylenchus* spp. and ectoparasitic nematode species, has been more elusive. This is consistent with observation in our research. Eleven genotypes were highly resistant to both populations of *M. hapla.* Conversely, most genotypes were as susceptible to *P. penetrans* as 'Totem', a susceptible cultivar. Among the limited number of populations of *Fragaria* evaluated in this research, *F.* ×*ananassa* genotypes ranked among the most resistant to both nematode species. Integrating nematode resistance into horticulturally superior cultivars should be more rapid for *M. hapla* than for *P. penetrans.* In regions where *M. hapla* is a limiting factor to commercial production, this research identifies germplasm that is useful in developing resistance in breeding material. As several of the commercial cultivars showed good resistance to *M. hapla* and *P. penetrans*, there would be minimal value in returning to native germplasm as a source of resistance.

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